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October 6, 1965 GERA-1080

# NYSTAGMUS AND BODY CONTROL FOR INPUTS OF REPEATED PATTERNS

Robert Mayne
Manager
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This report is in partial compliance to a contract under the

National Aeronautics and Space Administration
Manned Spacecraft Center
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## SUMMARY

The report discusses nystagmus in the context of body control. It is indicated that body movements may be classified in accordance with the degree in which they are anticipated. Willed movements are fully anticipated, as are imposed movements of simple repeated patterns. These movements are said to be controlled by internal programs developed as the result of nulling out unpleasant conscious sensations. Other movements, such as those resulting from suddenly impressed acceleration, and illusory movements as in the post-rotational situation, are not predictable to the same degree. Nystagmus, as well as body movements, is said to be affected by the degree of prediction. There is no single transfer function which can define the response to various stimuli. Nystagmus is shown to consist of three components: the slow phase, the fast phase, and a broad eye movement designated here as the "leading eye movement" or "lem." It is shown that for an imposed sinusoidal movement within the frequency bandwidth of the canals, the nystagmus provides clearly defined fixating periods, while lem causes the gaze to lead the motion by an amount proportional to velocity. The hypothesis is advanced that this lead corresponds to the perceived shift of body axis and provides a reaction time delay to permit recognition of an object of interest during a head movement, stop nystagmus, and focus on the object.

It is suggested that differences in the modes of prediction under different test conditions may account for discrepancies between canal response and eyeball velocities during the slow phase of nystagmus.

## INTRODUCTION

It is well known that nystagmus is under the control of the vestibule. The correlation between stimulus input to the vestibule and nystagmus, however, is by no means simple. Some of the disturbing factors, such as arousal and adaptation, have been identified. But even when precautions are taken to minimize these effects, there remains unexplained variations of response.

This paper attempts to examine nystagmus in the context of the system of body control. The system is characterized by means of prediction and adaptation foreign to mechanical servos. It is hoped that some of the variations of nystagmic response may be related to different modes of prediction under different situations.

The paper emphasizes total prediction which is believed to occur in the case of willed movements or in the case of imposed movements of simple repeated patterns. When a record of nystagmus is examined, it is found to consist of three components: the well-known slow and fast phase nystagmus, and a broad eye movement. This movement can be shown to cause the gaze to lead the sensed velocity, at least in the case of totally predicted movements, and for this reason it is called the "leading eye movement" or "lem." In other cases of imposed movement on the body, it appears to lag sometimes the sensed velocity. No references were found in the literature about lem, but when it was mentioned during a visit to Dr. G. M. Jones, he brought out some beautiful recordings of the movement taken some years previously as part of an unpublished study. The movement is mentioned, also, in a recent paper by Doctor Jones and J. H. Milsum[24] and it appears that the authors have also reached the conclusion that this movement leads in the direction of velocity. It is hoped that Doctor Jones' more complete study will be published soon.

The likelihood of such a movement was suggested some years ago by Mayne (1952),[28] in a paper which attempted to account for the audiogyral illusion. It was postulated, then, that the shift of the judged origin of a sound in a direction opposite to the sensed rotational velocity during a post-rotation period was caused by a shift in the sensed body axis in the direction of velocity. It seemed reasonable, at the time, to expect that an unconscious shift of gaze would take place to harmonize the sensed position of the body with respect to the environment as determined either by sight or by the system of spatial representation. It appeared, also, that a shift of the sensed position of an object in the oculogyral illusion in the direction of velocity, or in a direction opposite that of the audiogyral illusion, could be explained by the same movement. It was not perceived at the time, however, that these two requirements are contradictory. No good evidence of the movements was found in the literature and the problem was dropped because of press of other business. When study was resumed and various new references were consulted, it became apparent that nystagmus responds differently to different inputs; in other words, that different transfer functions, or different ratios between inputs and outputs, are applicable to different inputs. It is proposed to examine the possibility that the differences are the result of different predicting mechanisms operating under different conditions.

This paper emphasizes the class of movements under a fully predicted input, as in the case of a willed movement when the system generates the input in the form of a central nervous system (CNS) program, or in the case of an impressed movement of a relatively simple and repeated pattern, such as a continuous simple harmonic motion. Other types of inputs will be examined in later reports.

## NYSTAGMUS AND THE LEADING EYE MOVEMENT

### The Function of Nystagmus

It is well known that the slow phase of nystagmus under normal head movements has the effect of providing for successive fixation periods. During these periods the eyes turn with respect to the head at a speed equal and opposite that of the head in space. They remain, therefore, fixed in space, providing a short period of time when the image is stationary on the retina. For clear vision and recognition it appears that the fixation period should not be less than about

0.180 second. This requirement can only be met below a certain velocity of the head. For a normal maximum amplitude of 20 degrees of eye motion this velocity should not exceed $\frac{20}{0.180} = 110$ degrees per second. Nystagmus occurs, however, at higher head speeds under the apparent logic of the system that some slowing down of the image on the retina is better than none. Since the angle of sight, including both central and peripheral vision, is much greater than the maximum angle of rotation of the eyeball during succeeding fixating periods, the entire scene will be surveyed during a turn of the head. It can be surmised that if an object of special interest is spotted during the turn, the eyes will immediately focus on the object, using the optokinesthetic mode of control, and that nystagmus will stop.

## Accuracy of Nystagmus Control

Great accuracy is not needed in the control of nystagmus. A small drift of the image on the retina can be tolerated and it is found, accordingly, that the threshold of velocity for nystagmus is about three times as high as for sensation.[16,17] Groen[17] stated that the vestibule is not a very precise instrument. This comment is based on observations of discrepancies between body velocity and the slow phase velocity of nystagmus under conditions at wide variance from normal body movements. It is believed that these discrepancies must be accounted for in terms other than lack of accuracy. But it is true that even under the best conditions nystagmus does not appear to be controlled so as to offset very precisely the motion of the head during fixating periods. Such precise control is not essential if the object of the nystagmus is only to make possible the recognition of an object of interest during a turning movement of the head. Optokinesthesis can provide the fine accuracy which may be required to focus on the object once it is recognized and nystagmus has stopped.

The limitations in accuracy appear to be in the control of nystagmus, not in the signal provided by the canals. The canals, themselves, must operate with high precision in the control of body movements, such as in the performance of an acrobatic somersault, and are needed in providing accurate coordination of normal body activity. As indicated by Johnson, et al,[22] "... evidence of lack of smooth coordination of body movements, particularly noticeable during running and jumping," was found in monkeys having suffered bilateral labyrinthectomies. Bekesy[1] mentions that the cupula has about 3500 fibers associated with it, while the auditory nerve has about 35,000 fibers. This appeared to him as a disproportionate number of fibers for the cupula, where the ratio of threshold-to-maximum amplitude is about a hundred as compared to a million for hearing. In the first place, it is likely, as indicated in an earlier report,[31] that thresholds and limens determined on the basis of verbalization of just noticeable differences (j.n.d.) do not correspond to the resolution of the system in the unconscious control of body movements. In the second place, the data of the canals, as indicated in the same previous report, must be linear to be useful while sound data can be compressed logarithmically or otherwise without significant loss of function. The figures quoted support the previously expressed view[31] that the Weber law does not apply to vestibular signals, and that for the useful range of the canals equal stimulus increments are required to produce equal increments of sensed velocity. We cannot but pause here to reflect upon the extravagance with which the biological system provides distinct channels of information.

## Nystagmus Response under Experimental Situations

It is true, however, that under certain conditions of tests, such as steady acceleration over a protracted period, or during the post-rotational period, the slow phase nystagmus shows wide variations with the predicted velocity indicated by the canals as computed from the simple differential equation proposed by Steinhausen and investigated by others. Most troublesome is the discrepancy in time constants between the two types of response. Cupulometry measurements, for instance, give a time constant of about eight to ten for the decay of the sensed magnitude of velocity, and about twice this value for nystagmus.[16,17] Brown and Crampton[2] proposed an empirical formula relating nystagmus to a given input under conditions of protracted constant angular acceleration. One may be tempted, on the basis of this evidence, to conclude that there is one type of response for nystagmus and one for sensation. (Incidentally, we should distinguish between three phenomena which are usually designated by the same word "sensation," the conscious sensed magnitude of a modality of experience as of velocity or acceleration, a feeling, possibly of discomfort, possibly of interest, and the sensory data which is utilized in the unconscious control of body movement, all related to the same objective stimulus.) Guedry[19] shows that the discrepancy disappears for conditions approximating normal body movements. The data of Niven and Hixson[40] on nystagmic responses for various frequencies show that this response can be determined quite accurately from the simple differential equation proposed by Steinhausen.[44] The consistent time constant obtained on this basis for different frequency inputs is of the same order of magnitude, from seven to ten, as that obtained by sensation cupulometry. As will be pointed out later, other experimental data by Bekesy[4] lead to the same conclusion. It cannot be said, therefore, that two specific responses are associated, one with the sensed magnitude of velocity and one with nystagmus. Under conditions of sinusoidal input, the two responses appear to be identical. It is the purpose of this and succeeding reports to examine the possibility that a variable mode of prediction in addition to adaptation and state of arousal contributes to the observed variability between stimulus and response under different test situations.

## The Leading Eye Movement

The leading eye movement, like the nystagmus, responds differently to sinusoidal and other forms of input. We will primarily consider here the response to sinusoidal movements as representative of a class of totally predicted inputs.

Experimental evidence taken from data published by Niven and Hixson[40] will be presented later to show that for a sinusoidal input within the frequency response of the semicircular canals, the over-all effect of nystagmus and lem is to produce both a series of fixating periods with the eyes stationary in space, and a shift of the gaze in the direction of velocity. If we assume that the shift of gaze is not taken into account in the kinesthetic computations of position, the effect should be to locate objects as displaced in a direction opposite velocity if the body is taken as reference, or to locate the body as displaced in the direction of velocity if the environment is the reference.

It can be speculated on teleological grounds that this shift of the location of the body corresponds to the shift in sensed body axis, as discussed in earlier reports.[30,31,35] The location of the body with respect to the environment by sight would then correspond to its location by means of the system of spatial representation, with a shift of sensed body axis. Also, a lead in the direction of the gaze during a movement of the head would provide for a reaction time delay to be used in recognizing an object of interest, stopping nystagmus, focusing optokinesthetically on the object, starting to track the object, and possibly stopping the head movement. It will be noted, however, that if the gaze were always shifted ahead in the direction of sensed velocity, the displacement of an object in the oculogyral illusion would be in a direction opposite that actually observed. Lem, like nystagmus, requires a different treatment for different experimental situations.

## SOME BASIC PRINCIPLES OF MECHANICAL AND BIOLOGICAL CONTROL SYSTEMS

Nystagmus is part of the over-all system of body control and, therefore, is probably subject to the same basic principle of operation. A brief review of the operation of this system insofar as it is understood is, therefore, pertinent to the problem at hand. We may begin the discussion by reviewing some of the characteristics of mechanical systems.

### Linear Prediction in Mechanical Control Systems

All control systems require a certain amount of time to react fully to a given stimulus, and the delay may introduce considerable error in the response. The flywheel governor of a steam engine, the automatic steering system of a steamship, the autopilot of an airplane, even the thermostats in our houses, are subject to this defect. In the worst condition, energy output from the system is fed as input so as to cause oscillation and a loss of function.

The defect can be minimized by prediction. If a change of load on a steam engine, the meeting of a large wave by a steamship, the encountering of a vertical gust of wind by an airplane, or a variation of the temperature outside our houses could be predicted, corrections could be instituted ahead of time to cancel out or minimize the effect of the variations of stimulus.

Perfect prediction of a random input is not possible by definition. But a degree of prediction can be achieved on the average by measuring the rate of change of the input and assuming that this rate will be maintained for a given period of time. This mode of prediction is utilized commonly in linear servo systems. Better prediction may be achieved by taking acceleration into account. Again, acceleration measured at any particular moment may be assumed to remain constant for another given period of time. The value of the stimulus after this period can be computed on the basis of this assumption, knowing in addition both the value of the stimulus and its rate of change. The control function may also include the rate of change of acceleration. Conventional servos seldom go beyond third degree prediction of stimulus. The best proportion of velocity, acceleration, and rate of acceleration functions which may be added to a stimulus input for most accurate control, knowing the nature of the stimulus and the characteristics of the control, can be determined formally by automatic control linear theory. But the basic principle of reducing error by prediction in an automatic control can be visualized very simply. If, for instance, we know in advance that the temperature outside our houses will drop at a certain time and at a certain rate, there will be a lesser change of temperature inside the house if we turn the rheostat up before the temperature actually drops. This is particularly true if we have slow reacting heating systems. Biological systems appear to use similar schemes of prediction when no others are available.

There is another basic problem in the use of automatic controls. The sensing instruments of the control make unavoidable errors in measuring the stimulus. This is usually expressed by saying that the signal input contains a certain proportion of noise. Under the assumption that the noise may be sometimes positive and sometimes negative, the ratio of signal-to-noise can be improved by averaging the signal over a period of time. This, however, has the effect of slowing down the response of the control, requiring a greater degree of prediction. Norbert Wiener[52] developed a theory making possible the computation of predictors capable of optimizing the performance of automatic controls and minimizing mean square error when the noise and frequency content of the signal, together with the frequency response of the control, are known. The choice of the mean square error as a criterion is no doubt governed by the fact that it makes possible a linear formulation of the problem. But it seems rather arbitrary to assume that the undesirableness of an error is proportional to the square of the magnitude. We will see later that the biological system makes no such assumption.

The Biological Control System

Early experimenters[7, 8, 9, 10, 11, 14, 45, 47] very naturally tried to apply mechanical servo theory to the control of human body controls. The experiments they devised came generally under the class of "tracking" or "compensatory" tasks. In the first, the operator would manipulate a control so as to follow a given input as well as possible. In the second, the control was manipulated to cancel out the input. The test setup may have consisted of a moving spot presented on a cathode ray tube (crt) and suitable controls. The position of the spot on the crt would be controlled by the input and the task of the operator would be either to operate the control so as to cause a second spot to remain centered on the first, or to compensate for the input and keep the spot centered. Both tasks are typical of those normally performed by mechanical servos.

Various types of inputs were used, including step, sinusoidal, and random. Severe discrepancies were found in the response to these various inputs on the basis of linear servo theory. The response to a sinusoidal function was particularly at variance to that expected from a mechanical servo. Below the normal high limit of frequency response of the human operator the response was in-phase with the input, with a small attenuation of amplitude. According to conventional linear theory, such response would have required a very much higher frequency response than that of the human servo. To avoid this disturbing situation, emphasis was placed on random input. The results were sometimes analyzed mechanically by cross-correlating the input with the output. The analysis showed that there was some 80 percent of true correlation between the two and a residue of 20 percent of noise. The analysis usually stopped with this conclusion.

To account for the response to pure sinusoidal function, Mayne[34] proposed the hypothesis that the human control system possesses non-linear prediction methods not usually found in mechanical servos. One such method appeared to be based on the simple assumption that what has occurred repeatedly in the past will occur again. The so called range effect observed by many experimenters[10] was evidence of this type of prediction. If an operator is asked to respond repeatedly to a step input of a given amplitude and is then presented a step of a different amplitude, his response will correspond to an amplitude between the preceding and the new ones. The system apparently had predicted that succeeding inputs would all be of the same magnitude. This was a useful prediction which made the response more accurate as long as the input did not change. When a different input was presented, the prediction system had to give weight to the possibility that it was an error and elected to respond to an amplitude between the previous and the new one, as the most probable correct response on the basis of available data, and its method of prediction. Predictability of a function should perhaps be expressed as relative to the mode of prediction.

Mayne[34] pointed out that if the response to a single step input is divided into two phases, the reaction time delay and the response proper, it can be shown that the latter part conforms to a linear servo response. It appeared, therefore, that the reaction time was utilized in computing an internal programmed input and that the movement was carried out in closed loop as a response to an internal input. This mode of response was discussed in an earlier paper.[30]

Programmed response appeared, also, to serve another function. A body movement in carrying out a specific task, such as jumping over a ditch, catching a ball, or simply walking, includes many component movements which must be properly harmonized. The eyes must supply data to many such component movements and must divide their time in securing such data. It would be, therefore, of enormous advantage if the role of the eyes could be limited to the collection of data, and the necessary movements to achieve a specific objective be computed and carried out without them. This is precisely what seems to happen.

Recognizing the merit of a system which would permit multiple utilization of the eyes through time sharing, Mayne[34] suggested that if the human operator should be given a single task, such as responding to a random function, and the eyes had nothing else to do except to observe the variations of this random input, they would enter into the closed loop control as proprioceptors so that reaction time delay would be eliminated with a resulting improvement in the performance of the control. This hypothesis and others were tested in two succeeding research programs.

These programs had for an objective the investigation of a pilot-aircraft system. The test setup included a simulated one axis of freedom airplane and suitable control for an operator. The simulation was acted upon by simulated random gusts of wind and the task of the operator was to maintain the aircraft as level as possible by means of a stick control. The simulated attitude of the aircraft was read on a crt. In the initial program the pilot was stationary; in a second program, roll was introduced to provide vestibular cues. In no case, however, was the hypothesis confirmed. No evidence was discovered of the eyes operating directly as proprioceptors in the closed loop control of the operator's hand movements. Instead, the following mode of operation was revealed.

The operator would set, unconsciously, a threshold of error below which a previously established program would continue unchanged. As the threshold was reached, and following a reaction time delay, a preset or programmed movement would take place to correct the program and cancel the error. A reaction time could be measured between reaching the threshold and the beginning of the change in the program. Some of the details of the dynamics of the situation cannot be discussed here, but it became obvious that this scheme had distinct advantages over a conventional servo system.

A conventional servo system may have utilized a Wiener predictor which would have minimized mean square error for the simulated random gust input. But there is a requirement of greater import than minimizing mean square error in a typical life situation. No catastrophic mistake must occur. The aircraft can be permitted to roll within certain limits, an automobile can wander over the road within a lane, an acrobat standing on his head at the top of a long pole can oscillate within certain limits, our body when standing erect can sway through a small angle, our ancestral apes for whom the system was supposedly adapted and perfected could also sway slightly as they walked on a tree limb. The mean square error means very little in all these situations. It is more important to avoid a catastrophy. Such a catastrophy could occur if, because of "noise" in the detection of position, the system would call for a correction opposite that required. If a driver, for instance, thinks his car is too far to the left in a lane of traffic when it is actually too far to the right, a crash may occur as a result of the wrong correction. This sort of disaster may be avoided by smoothing the signal over a period of time. This, unfortunately, has the effect of slowing down the servo reaction and may lead to another catastrophy because of too slow a reaction if an automobile from the next lane crosses over unexpectedly. The biological system is able to have its cake and eat it, too. The need for smoothing is avoided by setting a threshold above noise while preserving fast response for emergency situations. The system has, also, the advantage of minimizing the effort required in effecting control, and the minimizing of effort appears to be an ever-present goal of the biological system. This model of control system was simulated with an analog computer and was found to have a response to a random input almost identical to that of a man.

The price which has to be paid for these advantages over a typical Wiener filter is of small import to the biological system. It is only that the output does not correlate perfectly with the input and, as indicated, that there is a residue of noise in the linear correlation between input and output. But, again, the minimizing of catastrophies and required effort are of greater value to the biological system than any other linear control characteristic.

Responses to a Sinusoidal Input

Figure 1, reproduced from the report by Mayne,[34] shows the response of the hand in following a sinusoidal input presented visually. The response for the first few cycles as indicated in Figure 1(a) has definite lag characteristics such as may be found in a typical closed loop servo. For this reason the response was labeled "closed loop response." There are doubts, however, now that the response is of this type even in the initial period. Following a few cycles, the phase shift and the attenuation of the response nearly disappear for the frequency input of one cps as indicated in Figure 1(b). This response is labeled "synchronous response." The change of response can be ascribed to a change in the mode of prediction, which could be considered as a form of very fast adaptation. The system is predicting, then, that the oscillatory input which has been experienced for a few cycles will continue indefinitely. A program has been generated in the CNS to correspond to the visual input. It is not difficult to conceive of a mechanism capable of this type of operation. Mayne[34] used the analogy of an autopilot which would be provided with means of generating internal sinusoidal input functions of a varying frequency, amplitude, and phase. A pilot presented on a cockpit instrument with a sinusoidal external output generated from the ground could adjust these three values to follow indefinitely the external output if the latter remained unvarying. The accuracy with which the external output would be followed would depend on the ability of the pilot to detect phase and amplitude errors, and on the frequency response of the autopilot aircraft system as related to the frequency of the input. It is apparent, however, that a more accurate response to an unvarying sinusoidal input would be possible by means of this system than with a conventional closed loop system

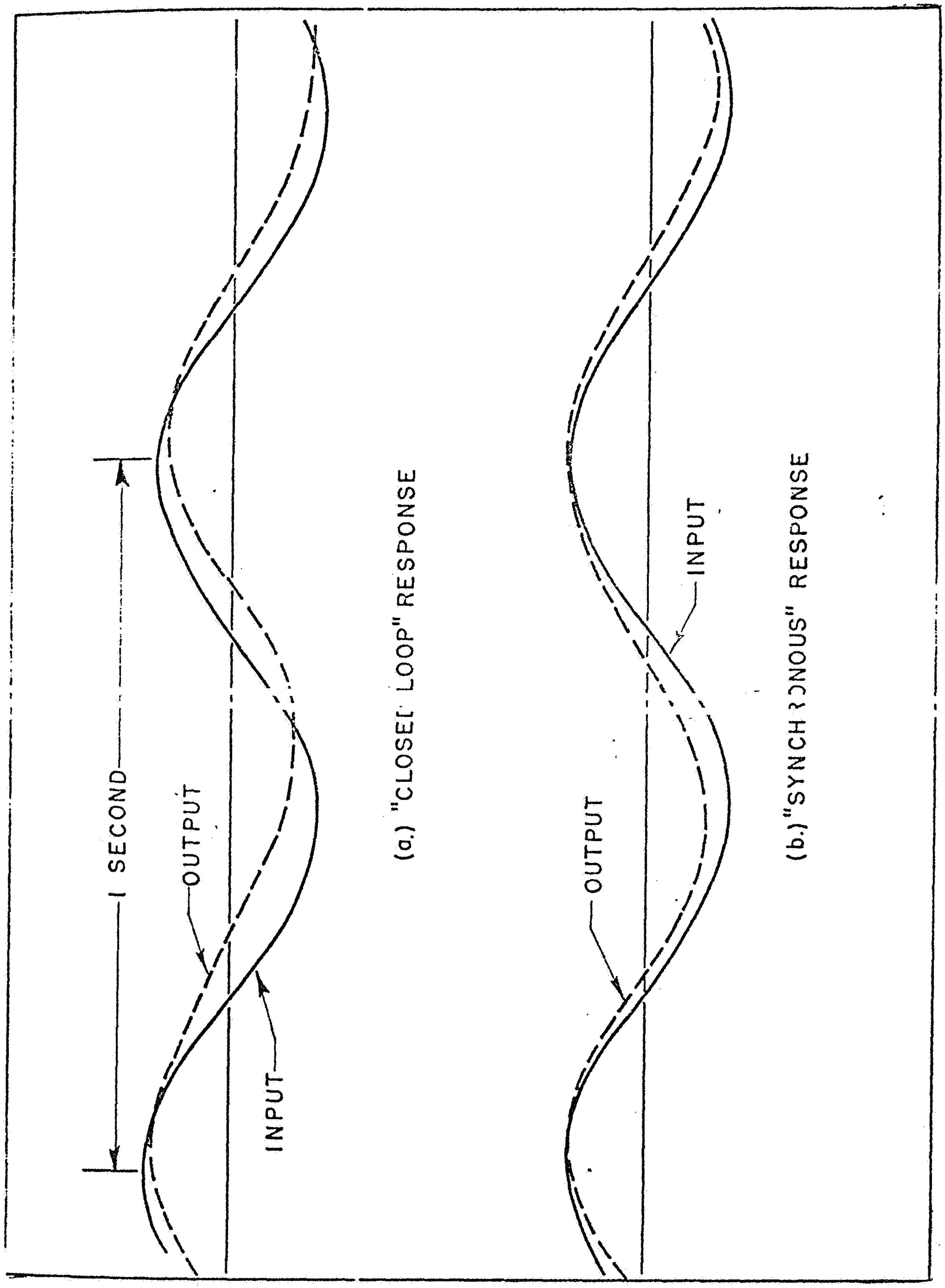



Figure 1. Typical response to simple sinusoidal input.*

*Reproduced from a report published in Electrical Engineering, March 1951 issue, entitled "Some engineering aspects of the mechanism of body control," by R Mayne.

of the same frequency response utilizing linear prediction. Because of this pilot-autopilot-aircraft analogy this type of response has been called sometimes the "autopilot response." The response to sinusoidal input is simply a special case of the response of the biological system through internal programming. Mayne[34] showed that the response to a repeated pattern of equally spaced step inputs of the same magnitude is also programmed in the same manner.

The response of the biological system is, of course, not as permanent as in the above analogy. As in all cases of the control of body movements, and of the relation of the biological organism to its environment, continuous adaptation takes place. There must be frequent checks of input versus output and corrections of the internal programming or the response will deteriorate, as can be demonstrated by simply closing the eyes.

It is interesting to note that data published by Jones and Milsum[24] regarding eye movements in following an oscillating target with head stationary show a phase shift and attenuation quite similar to that shown in Figure 1(b) for a frequency of one cps. The two test situations were similar in that they both included optokinesthetic sensing but differed in that the output of one was a hand and the other an eye movement. The findings of Young[53] in the analysis of eye movements of varying degrees of complexity, of Fender[13] in opening the feedback loop to optokinesthetic sensing, of Michael and Jones[39] in observing the response to a random stimulus, all fit into the broad context of body movements. It seems, therefore, that eye movements and nystagmus should be treated in this broader context.

Jones and Milsum[24] carried their experiments with eye response to frequencies beyond one cps. They showed that as frequency is increased, the amplitude ratio deteriorates faster than phase as would be predicted by conventional servo theory. The response depends on the ability of the system to detect phase and amplitude errors, onthe programming, and on the dynamic characteristics of the control system. It can be visualized that the adjustment of phase to match the input places less requirements on the system than the matching of the amplitude.

The human control system has received considerable attention of late from control engineers[5, 6, 27, 36, 37, 42, 51] in the analysis of various man-machine systems. The highly specialized mathematical techniques used in these analyses may have been an obstacle to the wide dissemination of their findings to physiologists and psychologists. It is hoped that the preceding simple discussion may suffice in providing a background for further discussion of nystagmus response.

## NYSTAGMUS RESPONSE TO A SINUSOIDAL INPUT

Nystagmus must be coordinated with body movements. It would appear, therefore, that the internal programming for a complex body movement should also include the input for nystagmic response. It appears from the previous discussion that programs are constructed not only for willed movements, but also for impressed movements of a simple repeated pattern. Such a program calls for no muscle reaction to move the body, but provides for proper anticipation of the movement and for control of the nystagmus. We will formulate later an hypothesis regarding the manner in which these internal programs may be constructed. A program for a sinusoidal impressed movement should be simple to construct and the nystagmic response should be quite similar to that of a "willed" movement in normal body activity.

Niven and Hixson[40] conducted an excellent series of experiments where nystagmus was measured for different frequency inputs. The data were analyzed by conventional control theory using LaPlace transform. The analysis showed that the response to various frequencies is very closely predicted by the theory in the way of phase shift and attenuation. The data make it possible to compute the time constant of the canals and give consistent results for various frequencies. On the basis of such data, it would be easy to conclude that the response is in direct closed loop control with semicircular canal input. Niven and Hixson[40] seem to assume that such is the case.

However, the steady-state response to a program such as indicated above cannot be distinguished from a closed loop response. It must be visualized that the subject is in the dark and has no information other than supplied by the vestibule, neglecting body reactions. He will interpret these data in terms of the adaptation which has taken place during normal body activity and body movements. These movements are within the bandwidth of frequency of the semicircular canals. If, now, a frequency below this bandwidth is impressed on the body, with no other sensory data available, the system would have no way of knowing that the vestibular signal is advanced in phase with respect to the input. It would interpret this signal as corresponding to a true body position. Any program that would be constructed on the basis of these data would also show the same phase shift. It would be interesting to oscillate a subject with eyes open for a substantial period of time at a frequency well below the normal frequency response of the canals, say, 0.05 cps. The phase of nystagmus with respect to the input oscillation could then be observed, first with eyes open, then with eyes closed. If adaptation had taken place, there would be no phase shift at this frequency, but a phase shift would be observed for a frequency such as 0.2 cps within the bandwidth of the canals.

Programmed response could be distinguished from closed loop response by observing the whole history of the response from the time the motion is first impressed on a subject, preferably a naive subject who had never been subjected to this type of test. A change of response as shown in Figure 1 would strongly suggest a programmed mode. Another critical experiment would be to stop the oscillation suddenly, perhaps at the point of zero velocity, and observe whether the response would continue for a while without external input. It must be noted that stopping a continuous oscillation, even at the point of zero velocity, will cause a sudden alteration to the velocity, or acceleration, pattern that will be detected by the system, causing a change in the programming. A reaction time would be required before the change could be effected.

As indicated above, the time constant of the system determined from Niven and Hixson's data[40] on nystagmic response at various frequencies is of the same order of magnitude as that determined by sensation cupulometry. This result would seem to indicate that for the conditions of test, there is no discrepancy between the sensed magnitude of velocity and vestibular response as observed by cupulometry during a post-rotational period or a protracted steady acceleration. Some observations by Bekesy[1] seem to confirm this view. Bekesy[1] noted the sensed point of reversal as reported by observers being oscillated at variable frequencies. These frequencies were below the normal bandwidth of the canals, and the sensation of reversal of the direction of turning shows a similar phase difference with respect to actual motion as that observed by Niven and Hixson[40] on the basis of nystagmus. The time constant determined from these two sets of observations would be, therefore, similar. The evidence seems clear, therefore, that there is no discrepancy between vestibular and sensory data under the conditions of an imposed sinusoidal motion on the body. It is believed the same conditions prevail for normal willed movements.

## PROGRAMMING OF BODY MOVEMENTS

### (An hypothesis)

We can find many examples of repeated patterns of movements during normal body activity. The simple act of walking is of this type. In other movements the pattern may occur only once. Our reaction to catch an object which has just slipped through our fingers before it falls to the ground is of this type. It can be speculated that such patterns are developed, stored in neural centers, and are activated by a triggering sensation such as caused by the object slipping from the hand. The search for the proper pattern takes place during the reaction time delay. We have suggested earlier that the organization of our body movements is governed by unpleasant sensations related to conflicting situations and that motion sickness is an exaggerated manifestation of these reactions. We have indicated, also, that the consequences of the conflicting situation, besides the conflict itself, is a significant factor in the unpleasantness of the sensation. As reported by Guedry and Graybiel[19] a coriolis illusion to the effect that the body is pitching forward is more unpleasant than one to the effect that it is pitching backward. This must be because the former illusion is more threatening than the latter. Sensations, themselves, were said to be alarm reactions usually triggered by conflicts. The bulk of body movements is controlled unconsciously without sensations, sensory data being utilized without creating conscious reactions.

We may try to be more specific regarding the manner in which programs are constructed with a tentative hypothesis.

When the body is first subjected to a sinusoidal impressed movement, as in the tests of Niven and Hixson,[40] the vestibular sensory data are unexpected and produce an unpleasant sensation. The system then generates a program which tends to null out this sensory input. When this input has been properly nulled, there remains a program which is the negative of the actual motion. Sensations disappear and certain body motions, in this case only nystagmus, are controlled by the program. The program can be advanced in time in the control of movements to provide prediction, but must also be timed properly to null out sensory output. There may be a place, therefore, in the system for the equivalent of delay lines such as used in electrical circuitry to provide proper timing for both functions.

We may speculate about the level at which the nulling out occurs. It may occur at the peripheral level through the existence of presynaptic nerve endings (Engstrom[12]), which could act as an efferent system in inhibiting vestibular output in a manner similar to the suppression of auditory nerve activity demonstrated by Galambos.[15] Body movements would then be controlled entirely by the program, and only vestibular outputs not being nulled out by the program would be taken into account. On the basis of this hypothesis, only sensory outputs which would not be so nulled, would produce sensations which, however, would not be necessarily unpleasant. They could be amusing or interesting.

A very significant experiment performed by Guedry and Graybiel[18] lends weight to this hypothesis. They found that subjects in a slow-rotating room would adapt after a certain time to movements of the head toward a shoulder. Originally, this movement had caused very strong sensations both of unpleasantness and of pitching either forward or backward. With adaptation, the sensations had disappeared. They reappeared when the room was stopped, but the sensed direction of pitching was reversed that previously observed for the same head movement. Guedry and Graybiel[18] concluded that "conditioned compensatory" reactions had occurred. On the basis of the present hypothesis, we could say that a program has been generated in the CNS to cancel out the sensory output. The program had also the effect of modifying the previously established response to the sensation of pitching forward or backward. Without the sensory output when the rotation of the room was stopped, the program was not nulled out and produced a reaction opposite that of sensory data alone.

Groen[16] expressed a view in accord with the programmed concept of body control discussed here to account for habituation to the movement of a ship by a passenger and for the acquisition of his sea legs. He writes in part, "(The passenger) having built the memory of the pattern (of the ship movements), the pattern center took hold of the automatic balance control and under guidance of the vestibular system registering movement, it allowed the test subject even to anticipate the coming movement." The further suggestion is made here that the pattern, or the program built up to cancel out the vestibular sensory pattern, provides precisely the information which is needed to counteract this motion. The vestibule, then, would function to maintain the accuracy of the programming, and would detect any deviations in body movement from that anticipated by the program. The sensation experienced by a passenger after disembarking is caused by the programming which is still in force and which is not cancelled out by sensory signals, and may be triggered by a random sensation similar to that experienced on board ship. It would be interesting to observe subjectively whether the sensation in this case is the reverse of the normal ship motion as in the case of coriolis.

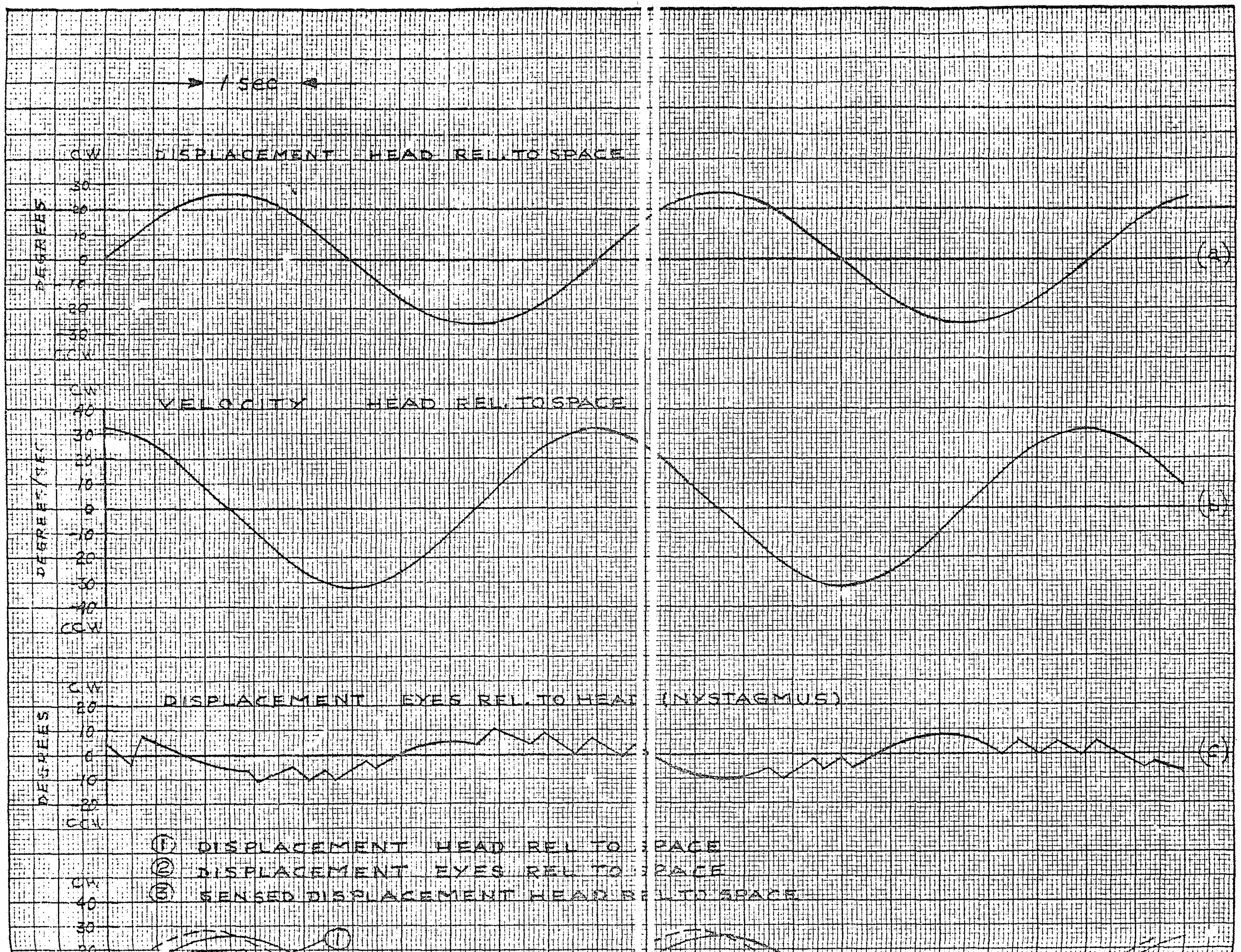
The control of body movements in accordance with this hypothesis differs somewhat from that suggested in an earlier report.[30] According to the present suggestion, all body controls would be by means of internal programming. The vestibule, like the eyes, would not act as proprioceptors, or feedback sensors in the control of body movement. They would only produce sensations and supply data for the construction of suitable programs. If bilateral labyrinthectomies cause a loss of coordination in monkeys as reported by Johnson, et al,[22] it would be because the normal monkeys could construct better programs because of the availability of more precise vestibular signals.

Obviously, considerable effort will be required to resolve some of the problems which the hypothesis raises. But it appears to hold considerable promise of clearing up other problems in the control of body movements. Somehow it appeals to the intuition of a control engineer.

## ANALYSIS OF DATA

For the purpose of illustrating nystagmus response to steady sinusoidal input, the data for an output frequency of 0.2 cps is taken from the paper by Niven and Hixson.[40] This frequency is well within the bandwidth of frequency response in a previous report.[31] The data in the report are reproduced at a small scale and errors may have resulted in various measurements. At the same time, the subject used in these experiments seemed to exhibit a lack of symmetry between clockwise and counterclockwise rotation. But the accuracy is believed good enough for the purpose of this report.

Figure 2 illustrates the analysis of these data. Figure 2(a) shows the displacement of subject's head relative to space versus time; Figure 2(b) the corresponding velocity. Figure 2(c) shows the nystagmus as taken from published data of Niven and Hixson.[40] Figure 2(f) shows a plot of the velocity of the eyes during the slow phase of nystagmus versus the velocity of space relative to the head. The correlation appears quite good and the error between the two may be accounted for in terms of lack of accuracy, either of nystagmus control or in the interpretation of the data.



1 SEC
CW
DISPLACEMENT HEAD REL. TO SPACE
DEGREES
30
20
10
0
10
20
30
CCW
(a)
CW
VELOCITY HEAD REL. TO SPACE
DEGREES/SEC
40
30
20
10
0
-10
-20
-30
-40
CCW
(b)
CW
DISPLACEMENT EYES REL. TO HEAD (NYSTAGMUS)
DEGREES
20
10
0
10
20
CCW
(c)
① DISPLACEMENT HEAD REL TO SPACE
② DISPLACEMENT EYES REL TO SPACE
③ SENSED DISPLACEMENT HEAD REL TO SPACE
CW
40
30
20

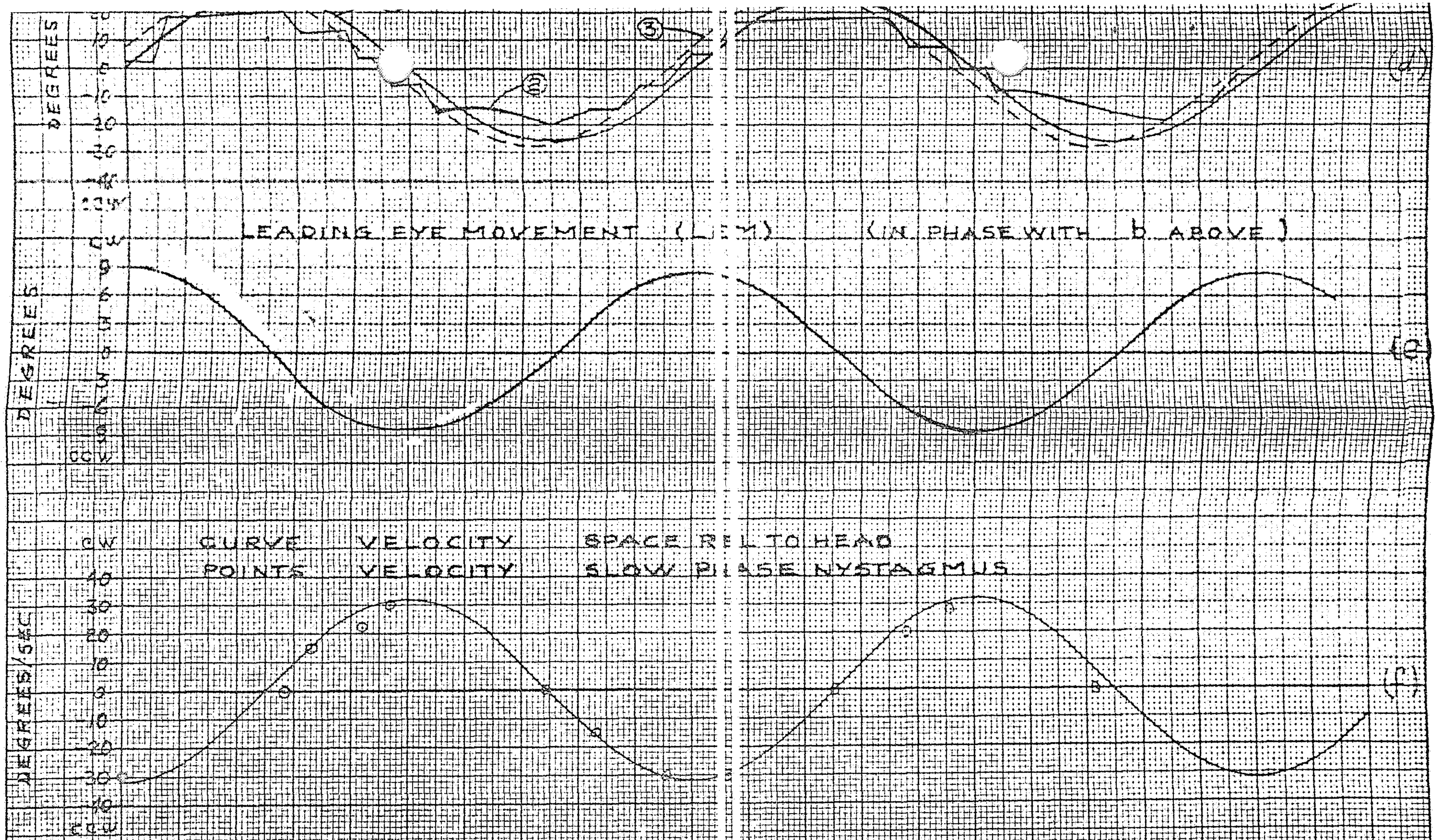



Figure 2 NYSTAGMUS RESPONSE TO STEADY
SINUSOIDAL INPUT.

Curve 2 of Figure 2(d) shows a plot of eye position in space. The plot shows that the eyes remain generally stationary in space during the slow phase of nystagmus and provide reasonably accurate periods of fixation, good enough to recognize an object of interest during a turn of the head. This curve corresponds to that published by Jones and Milsum[24] for the case of "head oscillating, eyes scanning stationary scene."

The point on the curve where the slow phase nystagmus begins corresponds to the direction of the gaze and does not correspond to body position at the same time. The difference is the result of lem. If, as postulated earlier, this eye movement is not taken into account in the optokinesthetic computations of eye direction, the position of the body with respect to the environment would be shifted accordingly. The shift would be maintained during the slow phase eye movement because this movement enters in the computations. If, therefore, a sine wave is drawn through the starting points of the slow phase of nystagmus, it will represent the average sensed position of the body with respect to the environment as determined visually. This curve shows that the gaze leads the position of the body. Curve 3 of Figure 2(d) shows the amount of lead during the cycle and indicates that the lead is proportional to velocity (Figure 2e), with a maximum of about 18 degrees. It will be noted that such lead at a frequency of 0.2 cps corresponds to a time advance of 0.25 second corresponding to a reaction time delay of average duration.

It can be speculated, as indicated earlier, that this lead may serve one of two related purposed, or both. It could harmonize sensed position established either visually, or through the system of spatial representation and/or could provide a reaction time delay to permit recognition of an object during a turn of the head, stop nystagmus, focus on the object optokinesthetically, start a tracking mode of response of the eyes, possibly stop the head movement, and initiate other appropriate measures. Further experimentation is required to establish more definitely the characteristics and integrated functions of this shift.

## Discussion

The response of nystagmus to a sinusoidal input of motion impressed on the body appears to be fully accountable in terms of the simple differential equation proposed by Steinhausen.[44] There appears to be no discrepancies between the velocity of slow phase nystagmus and the sensed characteristics of the motion in the way of amplitude and phase. The response is believed to correspond to normal willed movements of the body in that the input is fully anticipated and internally programmed. It is believed, accordingly, that in normal willed body movements there is also full agreement between sensory data and nystagmus.

The control of nystagmus is believed to be governed by the same laws as other body movements and should be investigated within this broader context. Present evidence is to the effect that all body movements are carried out by internal programming, and that nystagmus is similarly controlled. Simple experiments are needed to confirm this view in the case of sinusoidal impressed movements on the body. Such experiments would simply call for an observation of the initial response to the stimulus, and the response to its sudden cessation, besides the steady-state response which is usually observed.

The programmed control of body movements is part of a much broader field in the realm of behavior. It is a manifestation of a tendency of the organism to refer as much of behavior as possible to the autonomic control of the body. It probably includes the conditioning of reflexes, the programming of spoken and written language, the memorizing of a musical melody, the formation of habits, learning, etc. A better understanding of nystagmus may be possible when viewed in the broadest possible context.

Mayne[34] wrote, "Motions of the body become amenable to the discipline of control and communication engineering after they have been learned (programmed)." The process of learning and programming, however, transcend these disciplines. Experimental evidence is that they include such phenomena as sensations, feelings, and state of arousal, goals which find no counterparts in the mechanical system. It is in this complex interaction of the psychological and the physiological fields that the solution to problems related to simple nystagmus and feelings of nausea must be sought.

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